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A report on the distribution of small mammals from Namibia

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Abstract

A sample of small mammal species from 37 pooled localities throughout Namibia was used to assess ecological and zoogeographical distribution patterns. Multivariate techniques (Cluster Analysis and Principal Components Analysis) revealed an essentially ecological distribution based upon climate/ vegetation types within Namibia. Five major ecological areas are defined which correspond to previously described vegetation and zoogeographic regions.

Introduction

Searching for and recognizing patterns in nature is one of the fundamental endeavors of scientists. Spatial patterns of species distributions belong to the realms of ecology and biogeography. While the ultimate causes of species distributions are evolutionary and require historical explanations, identifying the patterns are an essential first step in the process.

Mammalian taxonomy and distribution in southern Africa are poorly understood (Dippenaar et al. 1983; Skinner and Smithers 1990). Analyses in southern Africa (Rautenbach 1978) and especially of Namibia (Coetzee 1983) have greatly increased our understanding of mammalian distribution patterns in this part of the African continent. Namibia represents a major portion of the Southwest Arid Biogeographic Zone. The fauna of this zone is considered to be quite distinct and to have had a long evolutionary history (Bigalke 1972).

The Natural History Museum of Los Angeles County (LACM) has an extensive collection (over 6,500 specimens) of mammals from Namibia. While these specimens have never been reported upon in the literature, Coetzee's (1983) did use the field identifications of some of these as a basis for his analysis of distribution patterns of mammals in Namibia. In our curation of this collection we noted that there were numerous misidentifications and errors. We have corrected these and use the revised material as the basis for the following analyses.

The major question we ask is "What geographic and/or ecological patterns can be discerned from the specimens from Namibia housed in the LACM?" Three Biotic Zones are recognized in Namibia by Skinner and Smithers (1990), Namib Desert, Southwest Arid, and Southern Savanna Woodland. These are the same as defined by Rautenbach (1978). Coetzee (1983) also recognized and defined these zones as mammalian Zoogeographical Provinces within Namibia. Since Coetzee (1983) had presented an analysis of mammalian distribution patterns in Namibia, we wanted to use the current material as a comparable sample. If the faunal areas recognized by Coetzee (1983) have biological validity, then an analysis of a subsample of mammals from Namibia should also reflect similar patterns. In addition we use the results of this analysis to suggest testable hypotheses concerning mammalian distribution patterns.

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Material and methods

Because the LACM collection concentrated upon small mammals, we restricted our analysis to the following orders, Insectivora Macroscelidea, Lagomorpha, Rodentia, and Hyracoidea. Mammalian taxonomy used herein follows that of Skinner and Smithers (1990) and Meester et al. (1986). However, these authors recognize but a single species of hyrax from Namibia, *Procavia capensis*. Because there are definite morphological differences in the specimens we have on hand we prefer to recognize two species for our analyses, *P. capensis* and *P. welwitschii*.

Localities were used as operational taxonomic units (OTU's sensu Sokal and Sneath 1963). Since several localities were represented by only a few species, we pooled nearby localities. Figure 1 is a map of the pooled localities. A list of the localities and species is given in tables 1 and 2. The pooled localities were used as the OTU's for the analyses.

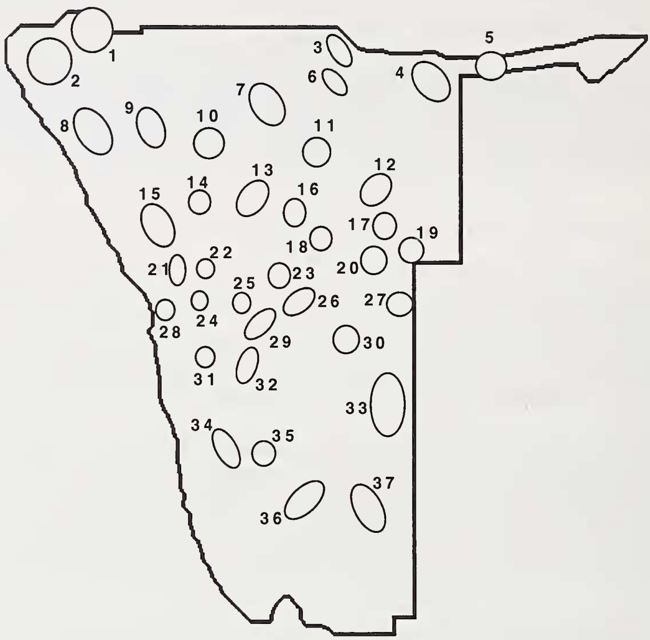

Fig. 1. Map of Namibia showing the pooled localities used in the analysis of mammalian distributions

Cluster analysis

Similarity between OTU's was calculated separately using the squared Euclidian distances and the "Faunal Resemblance Factor" (FRF) utilized by Coetzee (1983). The OTU's were clustered using the unweighted pair group method with arithmetic averages as suggested by Sneath and Sokal (1973). While both similarity matrices produced relatively equivalent groupings, the results presented here are based upon the squared Euclidean distances.

Principle components analysis (PCA)

OTU's were subjected to PCA, based upon a correlation matrix, to select an optimal subset of species (variables) from our sample that would bring about an ordination of the pooled localities. In order to simplify interpretation of the analysis, low PC scores are those OTU's which have a cummulative loading of less than −0.99 while high PC scores are those greater than +1.00.

All computations were done using an IBM/PC 386 using the SPSS statistical packages (Norusis 1988).

Table 1. **Collecting localities in Namibia**

Number in parentheses at end of locality indicates the pooled locality of Fig. 1

1. Kaokaland Area I; Opuwa, 106 km N, 65 km W Epupa Valley (1).
2. Kaokaland Area I; Opuwa, 66 km N, 84 km W Etengua (1).
3. Kaokaland Arae I; 63 km N, 55 km W, near Otjiangasemo (1).
4. Kavango Area I; Nkurrenhura, South Africa Police Camp (3).
5. Kaokaland Area I; 39 km N 130 km W Marienfluss (2).
6. Kavango Area I; 25 km N, 113 km W Rundu, Kanana (3).
7. Kaokaland Area I; Otju (2).
8. Kavango Area I; 9 km S, 84 km E Rundu, Shitemo (4).
9. Kaokaland Area I; Orumpebe (2).
10. Kavango Area I; 4 km S, 18 km E Andara, Bagani (5).
11. Kavango Area I; 81 km S, 73 km W Rundu, Tsotsana (6).
12. Kavango Area I; 66 km S, 113 km E Rundu, s fork nr N fork, Omuramba (4).
13. Tsuemb Dist; 45 km N, 33 km E Tsuemb, Wildernis 882 (7).
14. Grootfontein Dist; 80 km N, 93 km E Grootfontein, Tiervlei 1022 (6).
15. Damaraland; 6 km SE Sesfontein 207 (8).
16. Outjo Dist; 37 km N, 28 km W Kamanjab, Ermo 646 (9).
17. Tsumeb Dist; 40 km WNW Grootfontein, Ghaub Farm 47 (7).
18. Grootfontein Dist; 30 km ENE Otavi, Sumas Farm 746 (7).
19. Grootfontein Dist; 35 km E Omkrap 218 (11).
20. Outjo Dist; 41 km N, 45 km E Outjo, Pirre 345 (10).
21. Damaraland; Palmwag 702 (8).
22. Outjo Dist; Westfallen 245 (9).
23. Grootfontein Dist; 8 km S, 4 km W Otavi, Elephantenberg 792 (7).
24. Grootfontein Dist; 25 km S, 36 km E Grootfontein, Okamaruru 220 (11).
25. Damaraland; Krone 721 (8).
26. Hereroland East; 58 km N, 108 km E Otijinunu (12).
27. Otijiwarongo Dist; 52 km ESE Otijiwarongo, Okosongomingo Farm 148 (13).
28. Otijiwarongo Dist; 9 km S, 11 km E Kalkfeld, Elshorst 90 (14).
29. Otijiwarongo Dist; 78 km S, 48 km E Otijiwarongo, Ousema 201 (13).
30. Omaruru Dist; 35 km N, 27 km W Omaruru, Eausiro W 100 (15).
31. Hereroland East; 7 km N, 21 km E Otijinunu (12).
32. Okahanhdja Dist; 75 km N, 117 km E Okahanhdja, Kalidona 277 (16).
33. Omaruru Dist; 8 km N, 9 km W Uitspan 59 (= Kompanenosiid 59) (15).
34. Omaruru Dist; 18 km S, 6 km E Omaruru, Kamombande 86 (15).
35. Gobabis Dist; 117 km N, 39 km E Gobabis, Gelukwater 681 (17).
36. Omaruru Dist; Erongo West 83 (15).
37. Gobabis Dist; 67 km N, 82 km W Gobabis, Kambingana 204 (18).
38. Gobabis Dist; 64 km N, 103 km E Gobabis, Oostenwald 447 (19).
39. Karibib Dist; 17 km S, 7 km W Usakos, Naob 69 (21).
40. Karibib Dist; 47 km S Wilhelmstal, Okandukaseibe Farm 27 (22).
41. Windhoek Dist; 24–30 km N, 68 km E Windhoek, Okatumba South 149 (23).
42. Gobabis Dist; 41 km N, 2 km W Gobabis, Eava 383 (20).
43. Karibib Dist; Nordenberg 76 (21).
44. Karibib Dist; 35 km S, 3 km W Usakos, Dorstrivier 13 (21).
45. Windhoek Dist; 71 km ENE windhoek, Muambo 130 (23).
46. Windhoek Dist; 10 km N, 68 km E Windhoek, Springbock Valley 132 (23).
47. Karibib Dist; 73 km S, 3 km E Bethal Farm (24).
48. Gobabis Dist; 40 km S, 88 km E Gobabis, Uithou 366 (27).
49. Swakopmund Dist; 8 km E Swakopmund, Swakopmund River (28).
50. Windhoek Dist; 81 km SW Wasservallei 382 (25).
51. Windhoek Dist; 110 km E Windhoek, Arnhem Farm 9 (26).
52. Windhoek Dist; Autabib 100 (26).
53. Windhoek Dist; 10 km N, 31 km W Rehoboth, Naos 46 (29).
54. Rehoboth Dist; Wostel 256 (29).
55. Windhoek Dist; 9 km S, 59 km W Rehoboth, Isabis Farm 19 (29).
56. Gobabis Dist; 75 km S, 24 km W Gobabis, Mentz 65 (30).
57. Rehoboth Dist; Nauzerus West 229 (32).
58. Windhoek Dist; Solitare 412 (31).
59. Rehoboth Dist; Billisport 172 (32).
60. Mariental Dist; Mibela 200 (30).

Table 1 (continued)

61. Maltahoe Dist; 53 km S, 110 km W Maltahoe, Gorrasis 99 (34).
62. Mariental Dist; Asanib 294 (33).
63. Mariental Dist; vicinity of Twee River (33).
64. Luderitz Dist; 77–81 km WNW Helmeringhausen, edge of Kanaan Farm 104 (34).
65. Bethanie Dist; 23 km WNW Helmeringhausen, Barby Farm 26 (35).
66. Keetsmanshoop Dist; 89 km ENE Koes, Welverdiend Farm 328 (33).
67. Bethanie Dist; Odendorf 43 (36).
68. Keetsmanshoop Dist; Spitzkoppeost 159 (36).
69. Keetsmanshoop Dist; Gaibis 226 (33).
70. Keetsmanshoop Dist; Reinfels 125 (36).
71. Keetsmanshoop Dist; Naute 119 (36).
72. Keetsmanshoop Dist; Kochena 74 (37).
73. Keetsmanshoop Dist; Warmfontien 280 (37).

Results and discussion

Cluster analysis

Inspection of the dendrogram (Fig. 2) indicates that there are two major clusters and five minor clusters. Geographically, these are more easily shown in figures 3 and 4. Essentially, the two major clusters (Fig. 3) separate the country into west/southwest and northeast regions. The five minor clusters shown in figure 4 correspond fairly well with the Faunal areas described by Coetzee (1983) and to the vegetation types of Giess (1971). These five clusters are as follows (using terminology from Giess 1971): 1) Namib Desert, Southern Kalahari Desert, and Dwarf Shrub areas; 2) Escarpment and Mopane Savanna areas; 3) Mopane Savanna and Thornbush Savanna areas; 4) Highland Savanna; and, 5) Northern and Central Kalahari Desert and Karstveld areas. As can be seen in figure 4, there is a definite west to east gradient which reflects the climatic, vegetational, and geological differences in these areas (Coetzee 1983; Giess 1971).

Principle components analysis

The PCA, using 38 species (10 species could not be used because they were represented in only one locality each) as variables, was able to extract 33 principle axes. The first axis accounts for 15.3 % of the total variation. The second and third axes account for 9.4 % and 7.7 % of the variation, respectively. The first ten axes are necessary to represent 70 % of the variation. This indicates that the total variation is spred over almost all of the species distributions more or less equally. However, certain patterns can be recognized using the first axis alone.

As can be seen in figure 5, Principal Component (PC) I appears to be an east/west component. Low PC scores for the pooled localities occur in the west and south while high PC scores occur in the northeast. The distribution of PC scores corresponds with the distribution of clusters as discussed previously. Rainfall increases from west to east and south to north in Namibia (Coetzee 1983; Giess 1971). This would indicate that the First Principal Component is related to the ecological distribution of various species.

The distribution of representative high and low "loading" species on PC I are shown in figure 6. Species (variables) in this analysis had PC loading coefficients (Tab. 3) ranging from −0.61 (*Petromus typicus*) to +0.79 (*Mastomys natalensis*). Species with negative loading coefficients tend to be in the west and south while those with positive loading coefficients are in the northeast.

As we interpret these results, species with very low (negative) PC loading are more arid adapted while those with very high (positive) PC loading are more mesic. Species with low

Table 2. **Checklist of species**

Species names followed by a list of locality numbers from table 1

INSECTIVORA

1. *Crocidura cyanea* – 36, 40, 50, 55, 56, 57, 65.
2. *Crocidura fuscomurina* – 14, 29, 32, 38.
3. *Crocidura hirta* – 13, 14, 35, 37, 38, 46.
4. *Crocidura mariquensis* – 20.

MACROSCELIDEA

5. *Macroscelides proboscideus* 5 43, 61.
6. *Elephantulus intufi* – 1, 9, 14, 16, 18, 22, 24, 26, 27, 28, 29, 30, 32, 34, 35, 36, 37, 38, 40, 41, 46, 47, 48, 51, 54, 55, 59, 60, 65, 70.
7. *Elephantulus rupestris* – 9, 16, 39, 43, 44, 50, 55, 57, 58, 59, 67, 68, 72.

LAGOMORPHA

8. *Lepus capensis* – 10, 37, 39, 41, 44, 46, 47, 48, 56, 62, 66, 73.
9. *Lepus saxatilis* – 2, 12, 35, 40, 41, 46, 47, 48, 65, 68, 72.
10. *Pronolagus randensis* – 47.

RODENTIA

11. *Cryptomys hottentotus* – 6, 8, 9, 12, 14, 41, 42, 45, 48, 52.
12. *Hystrix africaeaustralis* – 40, 41, 46.
13. *Pedetes capensis* – 2, 10, 12, 13, 14, 16, 26, 29, 32, 34, 35, 37, 38, 39, 40, 41, 42, 47, 48, 51, 53, 55, 56, 63, 66, 68, 69, 73.
14. *Graphiurus murinus* – 12, 14, 26, 34, 53.
15. *Graphiurus platyops* – 44.
16. *Xerus inauris* – 16, 24, 32, 35, 41, 42, 46, 51, 55, 56, 58, 65, 66, 69, 72, 73.
17. *Funisciurus congicus* – 2, 15, 17, 20.
18. *Paraxerus cepapi* – 13, 17, 20.
19. *Petromus typicus* – 5, 40, 47, 50, 55, 57, 65, 67, 73.
20. *Parotomys brantsii* – 66, 69.
21. *Parotomys littledalei* – 49, 64, 65.
22. *Lemniscomys rosalia* – 6, 10, 14, 26, 27, 28, 31.
23. *Rhabdomys pumilio* – 25, 28, 36, 37, 40, 41, 43, 46, 47, 49, 51, 52, 53, 54, 55, 56, 57, 58, 59, 60, 62, 64, 65, 66, 67, 68, 69, 70, 72, 73.
24. *Zelotomys woosnami* – 26, 38.
25. *Mus indutus* – 4, 6, 8, 13, 14, 16, 19, 20, 23, 26, 27, 28, 29, 30, 32, 33, 34, 35, 36, 37, 38, 40, 41, 42, 46, 47, 48, 49, 50, 51, 54, 55, 56, 65, 66.
26. *Mus minutoides* – 8, 12, 37.
27. *Mus setzeri* – 12.
28. *Mastomys natalensis* – 4, 6, 8, 10, 11, 12, 13, 14, 16, 17, 19, 20, 22, 23, 24, 26, 27, 28, 30, 31, 32, 34, 35, 36, 37, 38, 40, 41, 42, 46, 49, 51, 52, 56.
29. *Mastomys shortridgei* – 20.
30. *Thallomys paedulcus* – 4, 6, 10, 13, 14, 15, 30, 34, 36, 40, 42, 47, 48, 55, 57, 59, 65, 66.
31. *Aethomys chrysophilus* – 1, 6, 8, 10, 11, 13, 14, 16, 17, 19, 24, 27, 29, 31, 32, 35, 37, 38, 41, 46, 50, 55.
32. *Aethomys namaquensis* – 1, 2, 3, 5, 7, 13, 16, 17, 20, 21, 22, 23, 24, 27, 28, 29, 30, 31, 34, 36, 37, 38, 39, 40, 41, 42, 43, 44, 46, 47, 48, 50, 51, 52, 54, 55, 56, 57, 58, 59, 60, 65, 67, 68, 72, 73.
33. *Desmodillus auricularis* – 5, 32, 35, 51, 62, 64, 65, 66, 73.
34. *Gerbillurus paeba* – 5, 12, 13, 24, 25, 29, 30, 31, 32, 35, 38, 39, 40, 41, 42, 43, 44, 47, 49, 51, 56, 58, 60, 64, 66, 68, 69, 71, 73.
35. *Gerbillurus setzeri* – 40.
36. *Gerbillurus tytonis* – 64.
37. *Gerbillurus vallinus* – 70.
38. *Tatera leucogaster* – 1, 2, 5, 6, 8, 10, 11, 12, 13, 14, 15, 16, 19, 20, 22, 23, 24, 27, 28, 29, 30, 32, 33, 34, 35, 37, 40, 41, 42, 43, 46, 47, 50, 51, 53, 55, 56, 58, 66, 69, 72.
39. *Tatera brantsii* – 31, 56, 66.
40. *Saccostomus campestris* – 6, 10, 12, 13, 14, 16, 22, 23, 26, 28, 29, 30, 32, 34, 35, 37, 38, 39, 40, 41, 47, 51, 52, 56.
41. *Malacothrix typica* – 16, 37, 42, 51, 55, 56, 65.
42. *Dendromus melanotis* – 12, 26, 31, 41, 46.
43. *Steatomys parvus* – 12.
44. *Steatomys pratensis* – 10, 14, 16, 26, 27, 28, 29, 41, 50, 55, 64.
45. *Petromyscus collinus* – 5, 7, 21, 22, 28, 39, 40, 44, 50, 57, 58, 67.
46. *Petromyscus monticularis* – 65.

HYRACOIDEA

47. *Procavia capensis* – 40, 51, 56, 65, 72, 73.
48. *Procavia weltwitschii* – 3, 5.

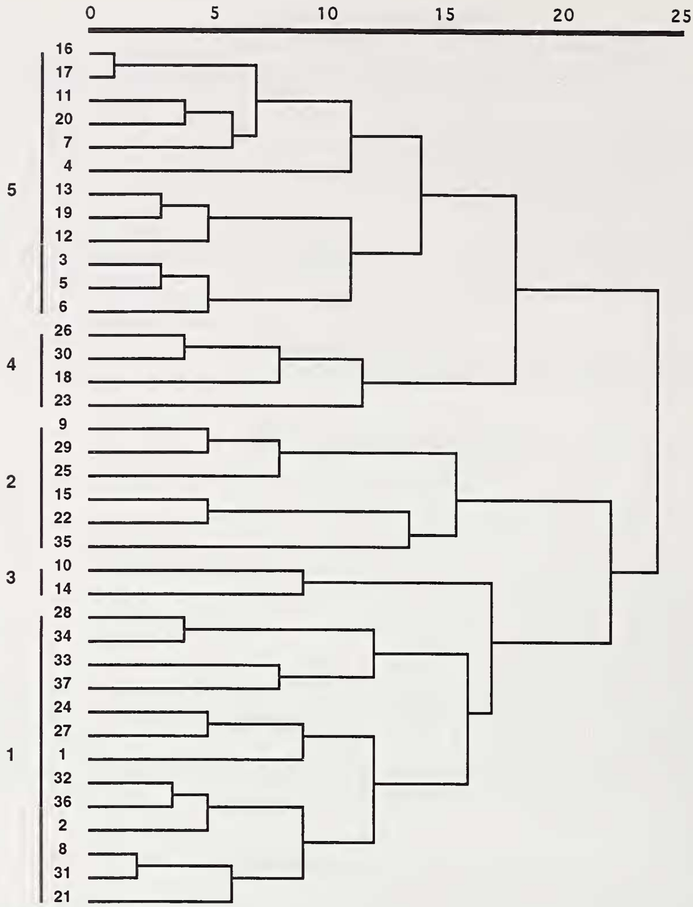

Fig. 2. Dendrogram of pooled localities showing recognized clusters. Numbers of minor clusters on the left. Major Cluster I includes 1, 2, and 3. Major Cluster II includes 4 and 5. See text for explanation

PC loadings include *Petromus typicus* (−0.61). *Elephantulus rupestris* (−0.56), *Petromyscus collinus* (−0.56), and *Rhabdomys pumilio* (−0.54). Rautenbach (1978) indicated that the first three of these species were restricted to the Southwest Arid and/or Namib Desert Biotic Zones. Species with high PC loadings include *Mastomys natalensis* (+0.79), *Aethomys chrysophilus* (+0.73), *Saccostomus campestris* (+0.72), and *Crocidura hirta* (+0.54). These species, while occurring in the Southwest Arid Biotic Zone, are also found in more mesic regions (Rautenbach 1978).

When the results of both the Cluster and PC analyses are considered together, the distribution patterns of small mammals are more clear. Cluster 1 (Fig. 3) represents the arid west and south of Namibia. Low PC scores for localities in these areas support this idea (Fig. 5), as well as, the low PC loadings for species (Fig. 6) that are considered to be restricted to arid regions. These species have a major portion of their distribution in the localities of Cluster I. Cluster II (Fig. 3) represents localities in the north and east of Namibia and have relatively high PC scores (Fig. 5). The species associated with this cluster are those with positive loadings and a more mesic ecological distribution.

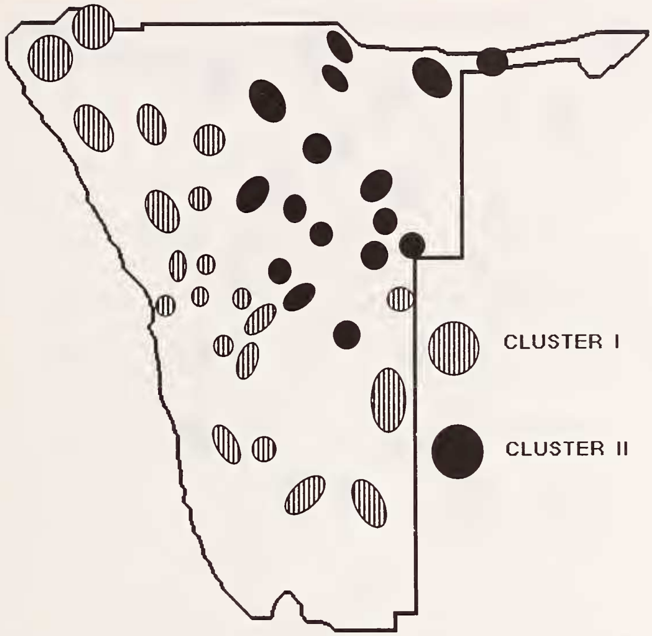

Fig. 3. Map of Namibia showing distribution of two major clusters

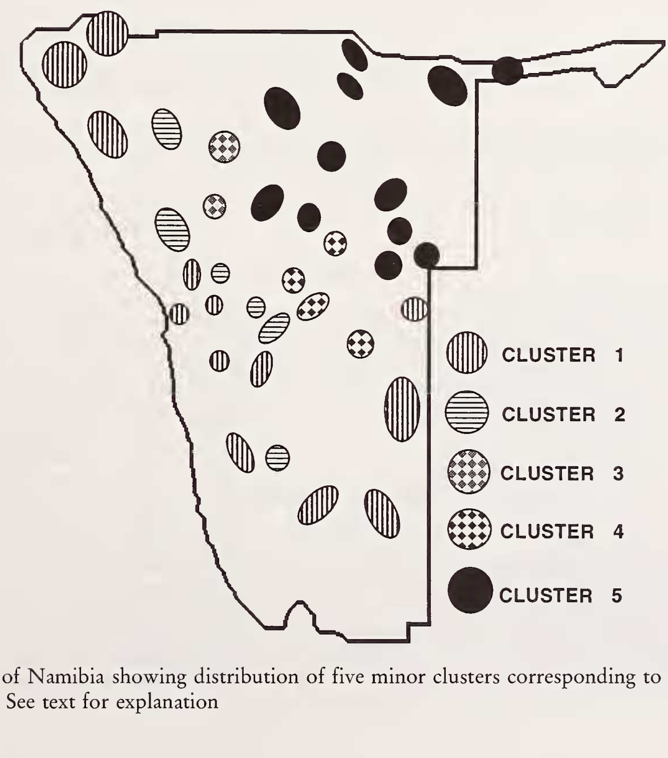

Fig. 4. Map of Namibia showing distribution of five minor clusters corresponding to vegetation and biotic areas. See text for explanation

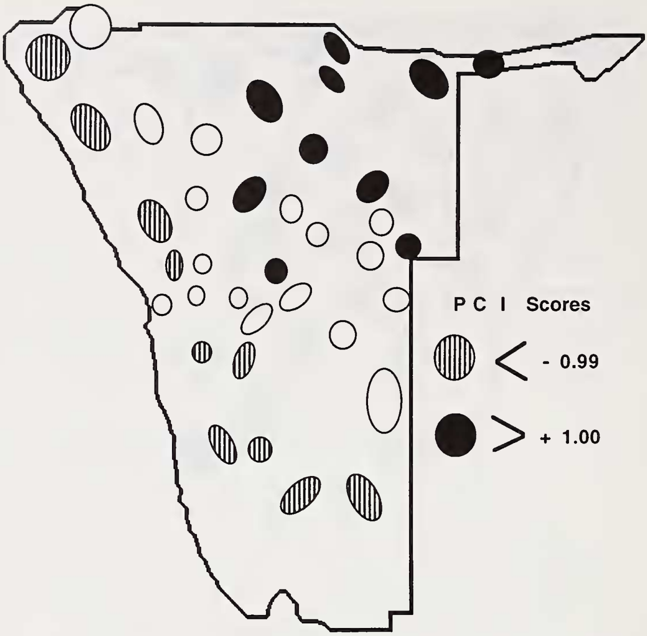

Fig. 5. Map of Namibia showing distribution of high and low PC scores for each pooled locality

Localities within Namibia that have intermediate PC scores contain a mixture of species. In addition, those species with intermediate loadings (between +/−0.50) are either widely distributed or have few locality records. Widely distributed species include *Gerbillurus paeba* (PC loading of 0.00 and occurring in 23 of the 37 pooled localities). Species with few locality records include *Parotomys littledalei* (PC loading of −0.31 and

Table 3. **First Principal Component loading coefficients for 38 species of small mammals in Namibia**

Coefficient/Species	Coefficient/Species
−0.61 *Petromus typicus*	+0.11 *Paraxerus cepapi*
−0.56 *Elephantulus rupestris*	+0.13 *Mastomys shortridgei*
−0.56 *Petromyscus collinus*	+0.21 *Tatera leucogaster*
−0.54 *Rhabdomys pumilio*	+0.23 *Tatera brantsii*
−0.34 *Crocidura cyanea*	+0.25 *Elephantulus intufi*
−0.31 *Parotomys littledalei*	+0.28 *Mus minutoides*
−0.30 *Aethomys namaquensis*	+0.32 *Steatomys pratensis*
−0.28 *Procavia capensis*	+0.37 *Zelotomys woosnami*
−0.27 *Desmodillus auricularis*	+0.40 *Graphiurus murinus*
−0.25 *Macroscelides proboscideus*	+0.45 *Cryptomys hottentotus*
−0.21 *Procavia welwitschii*	+0.45 *Dendromus melanotis*
−0.13 *Lepus saxatilis*	+0.47 *Crocidura fuscomurina*
−0.07 *Xerus inauris*	+0.48 *Pedetes capensis*
−0.05 *Thallomys paedulcus*	+0.50 *Lemniscomys rosalia*
−0.04 *Funisciurus congicus*	+0.50 *Mus indutus*
−0.03 *Malacothrix typica*	+0.54 *Crocidura hirta*
−0.03 *Lepus capensis*	+0.72 *Saccostomus campestris*
−0.00 *Gerbillurus paeba*	+0.73 *Aethomys chrysophilus*
+0.09 *Hystrix africaeaustralis*	+0.79 *Mastomys natalensis*

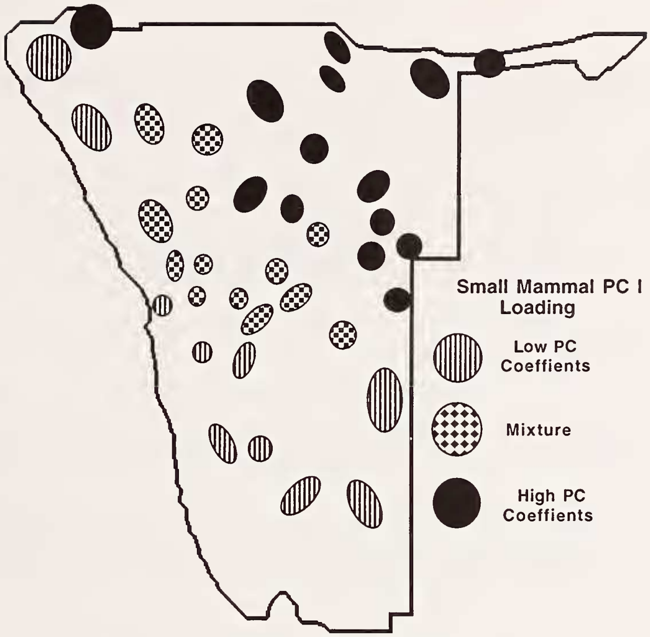

Fig. 6. Map of Namibia showing distribution of small mammal species that have high or low loading coefficients on the First Principal Component. See text and table 2 for species and explanation

found in only three localities of Cluster I) and *Zelotomys woosnami* (PC loading of +0.37 but found in only two localities of Cluster II).

While these results are based only upon a sample of the mammals from Namibia, they do reveal trends similar to those described by Coetzee (1983) and Rautenbach (1978). Bigalke (1972) and Morain (1984) considered southwestern Africa (including Namibia, parts of Botswana, and most of South Africa) to be an important biogeographic region because of the high amount of endemism. While our analyses would appear to represent more of an ecological distribution, it does confirm the zoogeographic analyses of Coetzee (1983) and Rautenbach (1978).

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We thank John Heyning, Sarah George, and Linda Barkley of the LACM for allowing us to work with the Namibia Mammal Collection. A major portion of this collection was aquired through the efforts of Lani Lester. The original expedition, October and November 1972, and a 1974 expedition were sponsored by Mrs. Reese Taylor. Additional specimens were obtained between 1974 and 1977. Travel funds to visit the LACM were made available through a San Jose State University Foundation, Faculty Development Grant and the Department of Biological Sciences, San Jose State University.

Zusammenfassung

Verbreitungsmuster von Kleinsäugern in Namibia

Eine Sammlung von über 6500 Kleinsäugern aus Namibia wurde genutzt, um ökologische und zoogeographische Verbreitungsmuster zu ermitteln. Über das ganze Land verteilte Einzellokalitäten wurden zu 37 Fundgebieten zusammengefaßt. Multivariate Auswertungstechniken (Cluster Analysis, Principal Components Analysis) ergaben klare ökologische Verbreitungsmuster, die den Klima- und Vegetationstypen von Namibia folgen. Fünf ökologische Hauptregionen lassen sich definieren, die mit bereits von früheren Autoren charakterisierten Vegetationszonen und zoogeographischen Regionen korrespondieren.

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